Migration patterns of Palaearctic *Acrocephalus* and *Sylvia* warblers in north-eastern Nigeria

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Abstract: OTTOSSON, U., F. BAIRLEIN & C. HJORT (2002): Migration patterns of Palaearctic *Acrocephalus* and *Sylvia* warblers in north-eastern Nigeria. Vogelwarte 41: 249–262.

In order to gather information on trans-Saharan migration strategies, phenology and energetics the passage of Palaearctic birds was studied in north-eastern Nigeria close to Lake Chad, in spring 1999 and in spring and autumn 2000. The ringing data and biometrics for six *Acrocephalus* and *Sylvia* warbler species trapped in sufficient numbers for statistical treatment are analysed with respect to inter-specific and intra-specific (age groups and sex groups) timing of migration, pre-migration fuelling and potential flight ranges. At take-off time in spring most birds carried fat loads that would carry them across the desert and in many cases well into Europe, whereas in autumn the birds arrived after the desert crossing with much lower fat scores. The results of a comparison with data from the same area collected in the late 1960s, when the climate was wetter than nowadays, suggest that the Common Whitethroat (*Sylvia communis*), a bird of arid habitats, may have adapted to the drier conditions and shifted its winter range southwards.

Key words: migration, Lake Chad, flight range, fat deposition, winter range.

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1. Introduction

Most insectivorous passerine birds that breed in northern Europe migrate to Africa during the winter. Many birds perform single migratory journeys of 5000 km or more and have to cross both the Mediterranean Sea and the Sahara (MOREAU 1972). Crossing wide ecological barriers may involve considerable risks to migrating birds. Many records exist of dehydrated and/or emaciated birds which have crossed deserts or oceans (e.g. SERLE 1956, JOHNSTON 1968, HAAS 1974). Since (with few exceptions) birds have no opportunity to feed en route they have to rely on stored fat and possibly also on favourable winds (ASH 1969, BAIRLEIN 1988, 1992, BIEBACH 1992, HJORT et al. 1996, KLAASSEN & BIEBACH 2000). The importance of stopover periods has only been fully realised in the last 10–15 years (ALERSTAM & LINDSTRÖM 1990, WEBER et al. 1994, SCHAUB & JENNI 2000). The rate at which energy stores can be accumulated at stopover sites appears to be one of the crucial factors determining the spatial and temporal organisation of migration. Depending on the availability of potential stopover sites, the journey may be broken up into a few long or several shorter flights. Thus, the time needed for migration is determined more by the time the migrants spend at stopover sites, than by the time it takes them to fly between these sites. Many long-distance migrants seem to be under selection to minimise the overall time spent on migration (ELLEGREN 1991, LINDSTRÖM & ALERSTAM 1992, KLAASSEN & LINDSTRÖM 1996, FRANSSON 1998), and, therefore, an ability to refuel quickly has evolved.

In Africa most Palaearctic migrant birds do not over-winter in the lush and seemingly rich forest areas, but rather further north in drier savannahs, often between 10–15° N (generally referred to as the „Moreau Paradox"; MOREAU 1972, ALERSTAM 1990). In recent years, concerns regarding trans-Saharan migrants have increased, since many of them are declining (COWLEY 1979, CAVÉ 1983, KANYAMIBWA et al. 1990, PEACH et al. 1991, MARCHANT 1992, SVENSSON 1997, 1998). For the Common Whitethroat (*Sylvia communis*), the decrease in breeding populations has been associated with drought periods in the Sahel (BERTHOLD 1973, WINSTANLEY et al. 1974, HJORT & LINDHOLM 1978, VAN DER HAVE 1991). Similarly, the population level and annual survival rate of Sedge Warblers (*Acrocephalus schoenobaenus*) are strongly correlated with rainfall in West Africa (PEACH et al. 1991, FOPPEN et al. 1999). However, the relationships between climate and population size are complex and much information is still needed for a full understanding of the population dynamics of trans-Saharan migrant birds.

In order to address questions about migration strategies and winter ecology of Palaearctic trans-Saharan migrants, we carried out a ringing programme in 1999 and 2000 just south of the Sahara, in the Sahel region close to Lake Chad in the north-eastern corner of Nigeria (OTTOSSON et al. 2001a). The study was placed where in the late 1960s the British Ornithologists' Union (BOU) had studied Palaearctic migrants (DOWSETT 1968, 1969, FRY et al. 1970, DOWSETT & FRY 1971). At that time the site was situated on the lakeshore, but it is now surrounded by farmland at the edge of an *Acacia* woodland which has colonised the area since the northern lake basin dried out during the droughts in the 1970–1980s.

2. Study area and methods

Bird-ringing was carried out at several localities close to the former Lake Chad Research Station of the Nigerian Federal Fisheries Service (13°33′N, 13°23′E), outside the town of Malamfatori. After a one month pilot study in April 1999, the main study period covered 6 months of fieldwork during 2000 (February-May and August-November). In the present analysis, we only use data from 2000, except in the comparison with body mass data from 1967 where data from both 1999 and 2000 are used.

The study area lies within the Sahel zone which, over the last 30 years, has been subject to increased desertification owing to a combination of decreased rainfall and increased human land use with overgrazing by the cattle population (JONES et al. 1996). The study area is a stopover site for migratory birds, both before and after their crossing of the desert and some, like the Lesser Whitethroat (*S. curruca*) and the Subalpine Warbler (*S. cantillans*), also winter there. We trapped birds with mist-nets in two different types of habitat, a „dry" and a „wet" one. In the dry area, vegetation was dominated by dense stands of Saltbush (*Salvadora persica*), up to 3 m high, with scattered *Acacia tortilis* and *A. senegal* and some *Balanites aegyptiaca* trees. The „wet" site was on the old lake bottom in more or less open country, with naturally inundated rice paddies or forest clearings used for farming. The main vegetation here consisted of *Mimosa pigra* and the recently introduced *Prosopis juliflora*, and some reed beds with *Phragmites* and *Typha*. Nets were set in or close to the water. Owing to changing water levels, various net sites were used. At both sites the nets were up before sunrise (05.30–06.00) and trapping normally continued until 09.00–10.00, depending on temperature and wind.

Birds were ringed with aluminium rings, wing-lengths were measured to the closest mm (maximum chord, SVENSSON 1992), and weights were taken to the nearest 0.1 g. Visible fat load was assessed by examining the subcutaneous fat in the tracheal pit and on the abdomen, on a 10-point scale, the 0–6 scale of HASSELQUIST & PETTERSSON (1985) extended by three scores, where 0 is no fat and 9 is most fat. This is similar to the scale used in the European Science Foundation's (ESF) Scientific Network on Western Palaearctic-African songbird migration (BAIRLEIN 1995, 1998), but with score 1 divided into two scores. Birds were aged and sexed according to SVENSSON (1992), JENNI & WINKLER (1994) and VALDENSTRÖM & OTTOSSON (2000).

Flight distances were calculated using Pennycuick's method (1989, programme 1 version 2) assuming normal air density at sea level, still air, an aspect ratio of 4.8 (the default for passerines in the programme) and a body drag coefficient of 0.1. To correct approximately for the fact that the increase in mass is not only due to fat, the distance generated was reduced by 25 % (c.f. HJORT et al 1996, OTTOSSON et al. 2001b). All statistical analyses were performed with SPSS 8.0.

The lack of birds from pentade 21, mid April, is due to a short non-ringing period owing to a change of personnel.

3. Results

Of the 42 species (with a total of 3171 individuals) of Palaearctic migrants trapped during the spring and autumn migration 2000 Great Reed Warbler (*A. arundinaceus*), Sedge Warbler, Reed Warbler

(*A. scirpaceus*), Subalpine Warbler, Common Whitethroat, and Lesser Whitethroat were trapped in numbers judged sufficient for more detailed analyses (more than 100 birds ringed; Table 1).

Table 1: Numbers of trapped birds of the analysed species for the year 2000.
Tab. 1: Fangzahlen der untersuchten Arten in 2000.

Species	Scientific name	spring 2000	autumn 2000	Total
Common Whitethroat	*Sylvia communis*	929	261	1190
Sedge Warbler	*Acrocephalus schoenobaenus*	703	334	1037
Reed Warbler	*Acrocephalus scirpaceus*	129	24	153
Lesser Whitethroat	*Sylvia curruca*	38	99	137
Great Reed Warbler	*Acrocephalus arundinaceus*	99	10	109
Subalpine Warbler	*Sylvia cantillans*	13	89	102
Total		1911	817	2718

3.1. Spring versus autumn occurrence

The Great Reed Warbler, Sedge Warbler, Reed Warbler and Common Whitethroat were more numerous in spring than in autumn, while the opposite was the case in the Subalpine Warbler and
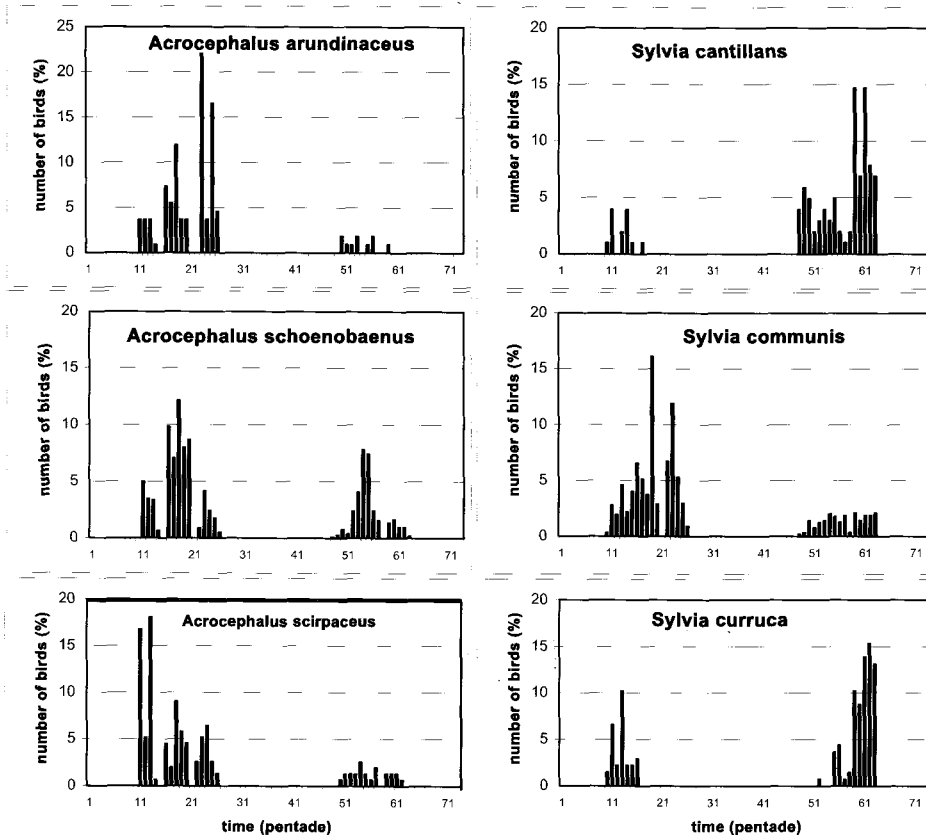

Fig. 1: Spring and autumn passage of Palaearctic warbler species at Malamfatori, Nigeria, in 2000. Pentade 1: 01–05 January.

Abb. 1: Herbst- und Frühjahrsdurchzug von paläarktischen Zugvögeln in Malamfatori, Nigeria, im Jahr 2000. Pentade 1: 01.–05. Januar.

Lesser Whitethroat (Table 1, Fig. 1). However, as the recorded passage of the Subalpine Warbler and Lesser Whitethroat were earlier in spring and later in autumn than that of the Common Whitethroat (Fig. 1), we may have missed part of their migration.

In spring, second-year Common Whitethroats passed on average 14 days later than the adults (Fig. 2; median test: $p < 0.001$), and Common Whitethroat males passed on average 23 days earlier than the females (Fig. 3), although this was statistically significant only in second-year birds. In all the other species, neither age nor sex seemed to affect the timing of spring passage.
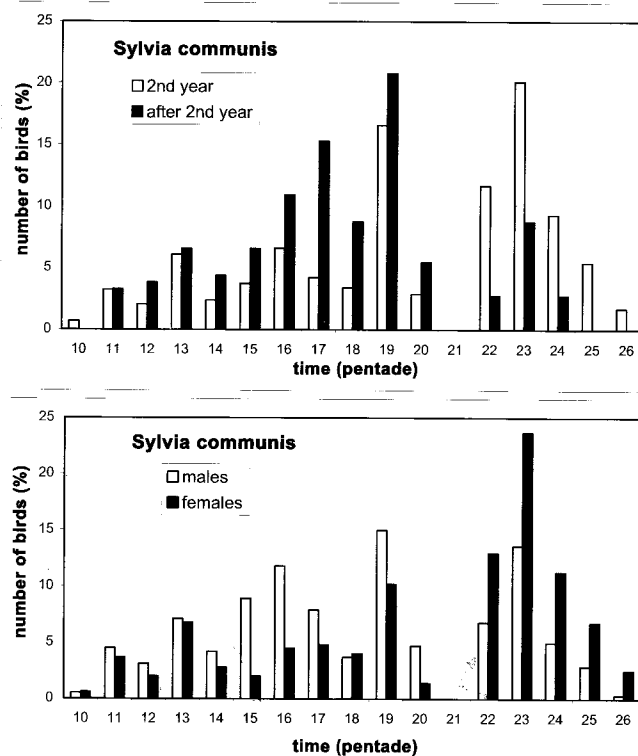
Fig. 2:   A: The passage of second-year (open bars) and adult (after second-year; black bars) Common Whitethroats in spring, shown as percentage of birds per pentade. Pentade 10: 15–19 February. B: The passage of male (open bars) and female (black bars) Common Whitethroats in spring.

Abb. 2:   A: Frühjahrsdurchzug von Dorngrasmücken in ihrem zweiten Kalenderjahr (offene Säulen) bzw. in späteren Jahren (schwarze Säulen). Pentade 10: 15.–19. Februar. B: Frühjahrsdurchzug männlicher (offene Säulen) und weiblicher (schwarze Säulen) Dorngrasmücken.
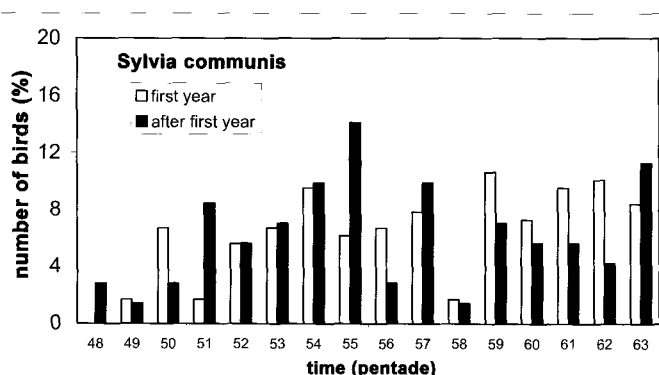
Fig. 3: The passage of first-year (open bars) and adult (black bars) Common Whitethroats in autumn. Pentade 48: 24–28 August.

Abb. 3: Herbstdurchzug diesjähriger (offene Säulen) und älteren (schwarze Säulen) Dorngrasmücken. Pentade 48: 24.–28. August.

In autumn, first year Sedge Warblers arrived significantly later than adults (median values 24 September for adults *vs.* 29 September for first-year birds; median-test, $p < 0.001$). In Common Whitethroats, no overall difference in the autumn arrival dates between the age groups seems to exist (Fig. 4) but within each sex adults arrived significantly earlier than the first-year birds (median values: males: 5 October in adults *vs.* 31 October in first-year birds, median test, $p = 0.001$; females: 26 September in adults *vs.* 6 November in first-year birds, median test, $p < 0.001$). In the other species, neither age nor sex showed any statistically significant influence on the mean arrival dates in autumn.
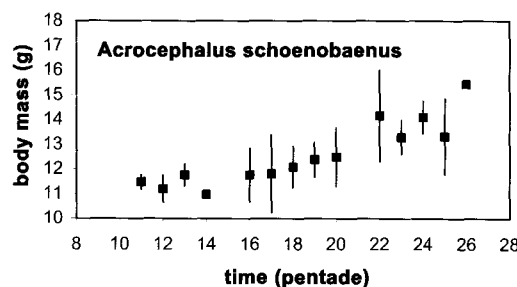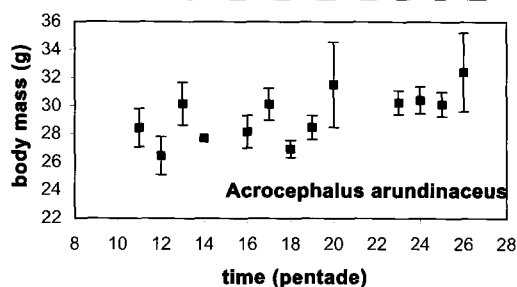
Fig. 4:   Variation of body mass in spring (mean ± s.e.), shown per pentade for the four most numerous species. Pentade 8: 05–09 February.

Abb. 4:   Saisonale Variation der Körpermasse (Mittelwert ± s.e.) der vier häufigsten Arten. Pentade 8: 05.–09. Februar.
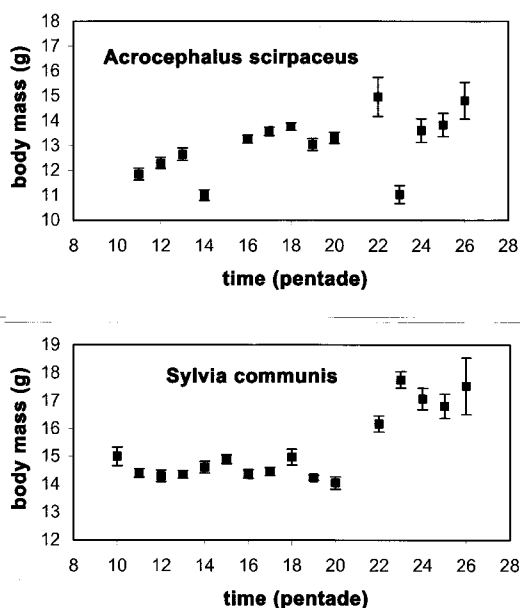
3.2. Wing length, body mass, and fat

A summary of biometrics for the six analysed species is shown in Table 2. Except for Subalpine Warblers, spring birds were clearly heavier than autumn birds. We conducted covariance analyses in order to account for size effects (i.e. wing length) on body mass, but except for the Subalpine Warbler and Great Reed Warbler the significant differences in body mass between spring and autumn birds were maintained (Table 2). This is also reflected in the differences in average fat load, where spring birds in all the six species analysed were significantly fatter than autumn birds (Table 2). The seasonal variation in body mass is not due to different age structures. In both Common Whitethroat and Lesser Whitethroat spring second year birds were significantly heavier and fatter than autumn first year birds (t-test; Common Whitethroat: $p < 0.001$, n = 587 and 179 respectively; Lesser Whitethroat: $p < 0.001$, n = 21 and 70 respectively), as was also the case in adult Common Whitethroats (t-test; $P = 0.016$; n = 181 and 65 respectively).

Besides between-season variation there was significant within-season variation in body mass and fatness in the *Acrocephalus* warblers and in the Common Whitethroat during spring passage (Fig. 5, Table 3). The average body mass increase in Common Whitethroat in spring was mainly due to a pronounced increase in body mass in birds caught from mid April onwards (Fig. 5).

Table 2. Biometrics (mean ± SD (N)) of some migrant Palaearctic *Acrocephalus* and *Sylvia* warblers at Malamfatori, Nigeria, in spring and autumn 2000.

Tab. 2:   Biometrie (Mittelwert ± SD (N)) paläarktischer *Acrocephalus* und *Sylvia* in Malamfatori, Nigeria, im Frühjahr und Herbst 2000.

|		Spring		Autumn		ANOVA	ANCOVA
Great Reed Warbler	Mass (g)	29.47 ± 3.78	(98)	27.76 ± 2.06	(8)	ns	ns
	Wing (mm)	96.64 ± 3.13	(99)	95.40 ± 1.08	(10)	ns	–
	Mass/Wing	0.305 ± 0.036	(98)	0.286 ± 0.023	(8)	ns	–
	Fat score	2.61 ± 1.62	(99)	1.20 ± 1.23	(10)	p = 0.009	–
Reed Warbler	Mass (g)	12.80 ± 2.41	(131)	11.04 ± 1.04	(18)	p = 0.003	p = 0.001
	Wing (mm)	67.09 ± 1.75	(129)	67.04 ± 2.00	(24)	ns	–
	Mass/Wing	0.191 ± 0.003	(129)	0.164 ± 0.003	(18)	ns	–
	Fat Score	4.24 ± 2.21	(131)	1.92 ± 1.41	(24)	p < 0.001	
Sedge Warbler	Mass (g)	12.20 ± 1.96	(689)	10.71 ± 0.79	(245)	p < 0.001	p < 0.001
	Wing (mm)	68.21 ± 1.94	(693)	67.41 ± 1.87	(330)	p < 0.001	–
	Mass/Wing	0.179 ± 0.028	(679)	0.159 ± 0.011	(242)	p < 0.001	–
	Fat Score	3.34 ± 2.13	(703)	1.63 ± 1.32	(333)	p < 0.001	–
Subalpine Warbler	Mass (g)	10.07 ± 1.47	(13)	10.17 ± 0.85	(86)	ns	ns
	Wing (mm)	62.36 ± 0,67	(11)	62.85 ± 2.20	(98)	ns	–
	Mass/Wing	0.164 ± 0.024	(11)	0.162 ± 0.012	(86)	ns	–
	Fat score	2.62 ± 2.02	(13)	1.58 ± 1.24	(88)	p = 0.012	–
Common	Mass (g)	15.39 ± 2.51	(912)	14.74 ± 1.04	(243)	p < 0.001	p < 0.001
Whitethroat	Wing (mm)	74.44 ± 1.72	(923)	74.86 ± 2.05	(261)	p = 0.001	–
	Mass/Wing	0.207 ± 0.033	(906)	0.197 ± 0.014	(243)	p < 0.001	–
	Fat Score	3.12 ± 1.99	(917)	1.69 ± 1.47	(260)	p < 0.001	–
Lesser Whitethroat	Mass (g)	12.54 ± 1.49	(37)	11.41 ± 0.84	(93)	p < 0.001	p < 0.001
	Wing (mm)	67.50 ± 1.55	(38)	67.48 ± 1.74	(99)	ns	–
	Mass/Wing	0.186 ± 0.021	(37)	0.169 ± 0.013	(93)	p < 0.001	–
	Fat score	2.68 ± 2.01	(38)	1.37 ± 1.22	(99)	p < 0.001	–
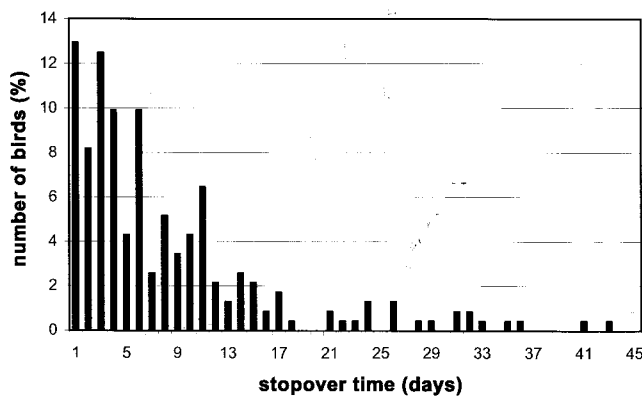
Fig. 5:   Stopover duration, all species combined, in percent per period (in days) in between catches.

Abb. 5:   Minimale Verweildauer aller Arten zusammen in Tagen.

Table 3: Within-season variation of biometrics derived from linear regression analysis of palearctic migrant *Acrocephalus* and *Sylvia* warblers at Malamfatori, Nigeria, in spring and autumn 2000. n = sample size, r = correlation coefficient.

Table 3: Saisonale Variation (ermittelt über eine lineare Regression) der Biometrie paläarktischer *Acrocephalus* und *Sylvia* in Malamfatori, Nigeria, im Frühjahr und Herbst 2000. n = Anzahl Vögel, r = Korrelationskoeffizient.

			n	r	p-value	slope
Great Reed Warbler	spring	wing length	99	0.1789	Ns	0.0125
		body mass	98	0.2706	0.007	0.2276
		weight/wing	98	0.2906	0.004	0.002
		fat score	99	0.2315	0.021	0.0841
	autumn	wing length	10	0.3850	Ns	0.1401
		body mass	8	0.0333	Ns	0.0221
		weight/wing	8	−0.0478	Ns	−0.0010
		fat score	10	−0.0612	Ns	−0.0255
Sedge Warbler	spring	wing length	693	0.0565	Ns	0.0308
		body mass	689	0.3357	0.000	0.1825
		weight/wing	679	0.3330	0.000	0.0026
		fat score	697	0.4094	0.000	0.2327
	autumn	wing length	330	0.1095	0.047	0.0742
		body mass	245	0.1157	Ns	0.0284
		weight/wing	242	0.0710	Ns	0.0284
		fat score	333	−0.0794	Ns	−0.0373
Reed Warbler	spring	wing length	129	−0.2050	0.020	−0.0747
		body mass	131	0.1999	0.022	0.1009
		weight/wing	129	0.2277	0.009	0.0017
		fat score	131	0.2807	0.001	0.1298
	autumn	wing length	24	−0.0450	Ns	−0.0265
		body mass	18	−0.3090	Ns	−0.0810
		weight/wing	18	−0.3370	Ns	0.0011
		fat score	24	0.0296	Ns	0.0117
Subalpine Warbler	spring	wing length	11	−0.1959	Ns	−0.0711
		body mass	13	0.1949	Ns	0.1425
		weight/wing	11	0.0764	Ns	0.0010
		fat score	13	0.4411	Ns	0.4418
	autumn	wing length	89	−0.3602	0.001	−0.1653
		body mass	86	−0.0985	Ns	−0.0171
		weight/wing	86	0.0599	Ns	0.0001
		fat score	88	−0.0321	Ns	−0.0083
Common Whitethroat	spring	wing length	923	−0.1504	0.000	−0.0659
		body mass	912	0.4202	0.000	0.2688
		weight/wing	906	0.4474	0.000	0.0038
		fat score	917	0.4708	0.000	0.2383
	autumn	wing length	261	0.0410	Ns	0.0201
		body mass	243	0.2544	0.000	0.0610
		weight/wing	243	0.2390	0.000	0.0007
		fat score	260	−0.3668	0.000	−0.1290
Lesser Whitethroat	spring	wing length	38	−0.2554	Ns	−0.2335
		body mass	37	−0.0388	Ns	−0.0342
		weight/wing	37	0.0111	Ns	0.0001
		fat score	38	0.3084	Ns	0.3653
	autumn	wing length	99	−0.0023	Ns	−0.0017
		body mass	93	0.0965	Ns	0.0366
		weight/wing	93	0.0766	Ns	0.0004
		fat score	99	−0.1379	Ns	−0.0702

3.3. Stopover time and body mass changes in retraps

For all species in this analysis, 275 birds (10 %) out of 2728 were retrapped at least once after the day of first capture, within the same season. In spring, the proportion of retraps was significantly higher than during the autumn passage (12.0 % *vs.* 5.0 %; χ^2-test: p < 0.001). Overall minimum stopover time of the species on record was short, with 50 % of retrapped birds having stayed less than 6 days (Fig. 6). Median stopover duration did not differ significantly between autumn and spring (spring: 6 days, autumn: 7 days), nor did the median stopover time during the spring passage differ between birds which gained body mass during stopover and those showing mass loss. But autumn birds gaining mass rested significantly longer than birds which lost mass (median duration of stay 13.5 *vs.* 3 days; median-test: p = 0.023).

For all species on record, 61 % of the spring stopover birds and 47 % of the autumn birds gained mass (Table 4). In Common Whitethroats the average gain of those birds that increased in mass was significantly lower in autumn than in spring, although similar maximum mass gains were achieved in both seasons.
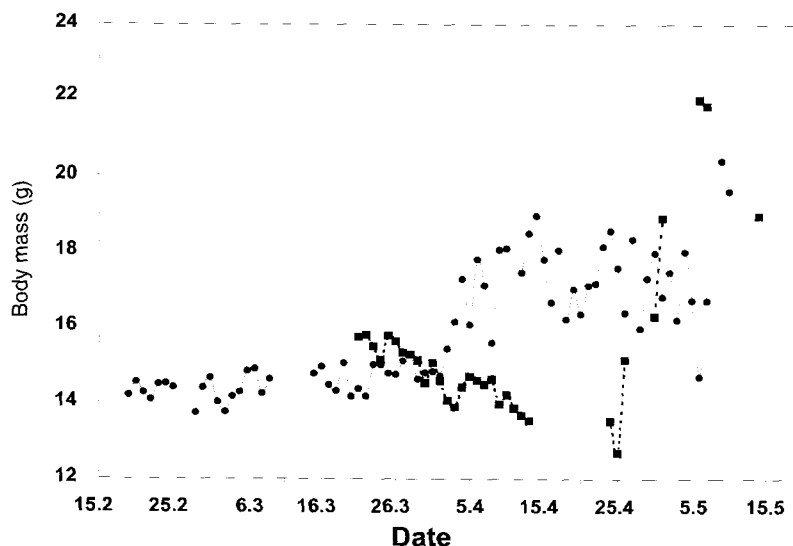

Fig. 6:   Average daily body mass of Common Whitethroats in 2000 (•), and during the BOU-expedition 1967 (■), from FRY et al. (1970).

Abb. 6:   Mittlere Körpermassen von Dorngrasmücken im Frühjahr 2000 (•) und 1967 (■) (aus: FRY et al. 1970).

Table 4: Statistics of body mass changes of retrapped Palaearctic *Acrocephalus* and *Sylvia* warblers.
Tab. 4: Körpermassenänderungen bei Wiederfängen paläarktischer *Acrocephalus* und *Sylvia*.

		all retraps				birds with weight loss				birds with weight gain				
		n retraps	% of first	median time	mean gain (g/d)	n	% time	median		n	%	median time	mean gain (g/d)	max. gain (g/d)
Great Reed Warbler	Spring	16	16,2	10,0	−0,26	9	60	9,0		6	40	10,0	0,24	0,60
Sedge Warbler	Spring	140	19,9	6,0	0,07	54	40	4,0		80	60	6,0	0,17	1,50
	Autumn	7	2,1	4,0	−0,41	4	80	4,5		1	20	0,13		
Reed Warbler	Spring	16	12,2	4,0	0,06	6	38	4,0		10	62	7,0	0,34	0,70
Subalpine Warbler	Autumn	11	12,4	10,0	−0,18	6	55	1,5		5	45	11	0,03	0,05
Common Whitethroat	Spring	57	6,1	4,0	0,07	15	27	3,0		40	73	4,0	0,25	1,04
	Autumn	20	7,7	13	0,04	7	39	6		11	61	21	0,14	0,95

4. Discussion

In the late 1960s the BOU-expedition trapped large numbers of birds in the same area in which we conducted our study (DOWSETT 1968, 1969 FRY et al. 1970, DOWSETT & FRY 1971). Despite major environmental changes since then, with Lake Chad almost disappearing from the area, our trapping figures were fairly similar to those of 30 years ago. The total number of birds of the species we studied was also higher during the spring than in the autumn (Table 1), and as expected most birds were heavier and fatter in spring (Table 2).

Differences in the timing of migration between species, and between age groups and sex groups, might reflect different migration strategies. However, according to our data, neither age nor sex seems to influence the timing of spring migration at this low latitude. But in Common Whitethroat, second-year birds migrated later than older ones, and males before females, a pattern similar to that found in northern Egypt (HORNER 1980).

At breeding areas, adult birds usually arrive before younger birds and the difference is most probably larger than the difference at onset of northward migration. This slower speed of migration is probably due to younger birds being less experienced than older birds (ELLEGREN 1991, 1993, FRANSSON 1995). In autumn, the adults migrate faster. Adult Common Whitethroats and Sedge Warblers arrived at Malamfatori on average significantly earlier than the juveniles, despite leaving the breeding areas approximately three weeks after the latter (Fig. 4; and FRANSSON 1995). From recoveries of both species (OTTOSSON et al. 2001a), and from the moult pattern of the Common Whitethroat (WALDENSTRÖM & OTTOSSON 2002), we know that the Common Whitethroats and Sedge Warblers trapped at Malamfatori originate from areas in the sector NNE of Lake Chad, and possibly come from populations in eastern Fennoscandia and western Russia.

4.1. Fuelling today and in the 1960s

Birds were on average heavier in spring than in autumn (Table 2) and all species carried more fat in spring than in autumn. The lack of proven increase in body mass in spring in the Subalpine Warbler and Lesser Whitethroat may be an artefact either of the small sample sizes, of the fact that part of their migration lies outside the study period, or because part of the fuelling of these dry-land species takes place north of our study area. For the Common Whitethroat the main increase in body mass in spring starts at the beginning of April and it intensifies from the middle of the month. The Sedge Warbler starts fattening earlier (Fig. 5). Why the mass increase in the Great Reed Warbler is relatively unpronounced we do not know.

If we compare the body mass data for the Common Whitethroat and Sedge Warbler with those collected during the BOU-expedition to the same area in 1967 (FRY et al. 1970), we find no overall increase in weight during their main period of activity from 22 March to 13 April, instead a decreasing trend in the Common Whitethroat (Fig. 6). However, some additional trapping after this period, until mid May 1967, showed an increase in average body mass for the Common Whitethroat more similar to that in the present study. But in 1967 this increase did not start until the end of April, about three weeks later than in 2000 (Fig. 6.). At Djoudj, in NW Senegal, the pronounced body mass increase for the Common Whitethroat during the 1990s started at the beginning of April, as in the present study (OTTOSSON et al. 2001b). The body mass curve for Sedge Warblers, which were trapped predominantly at wet sites away from the dry one where we trapped most Common Whitethroats, seems to be much more similar to what was recorded in 1967 and with a similar proportion of heavy birds (> 6.0g), which is 6 % in our data and was 5 % in 1967.

The earlier onset of migratory fuelling at Malamfatori either indicates that Common Whitethroats, unlike Sedge Warblers, nowadays start their migration earlier than they did 30 years ago, or that they now take-off for the desert-crossing from a more southerly location than before. There are some indications that the latter may be the case. FRY et al. (1970) believed that Common Whitethroat left the area northwards before achieving full pre-migratory body mass, since none of

the birds they caught between 21 March and 13 April exceeded 23 g. In the present study about 4 % of the Common Whitethroats weighed more than 23 g and 13 % had a mass of more than 20 g compared to only 0.6 % in the 1967 study by Fry et al. (1970). From Zaria (11°03'N 8°17'E), about 250 km further south than Malamfatori and in NW Nigeria, Fry (1971) noted that Common Whitethroats departed northwards before they started fattening, and at Zaria the maximum spring body mass was only 16 g.

The fact that a considerable proportion (ca. 30 %) of migrating Common Whitethroats trapped at Malamfatori after 1 May 2000 still had a body mass below 15 g (Fig. 4 in Ottosson et al. 2001a), indicates that also today some fattening takes place further north (our area was largely empty of Common Whitethroats by 10 May). But the proportion of birds continuing their fuelling north of this area may have been much higher in the wetter and perhaps less overgrazed 1960s, which could explain the difference shown in Fig. 7. A much smaller proportion of Sedge Warblers trapped in late April and early May had low body mass (Fig. 5 in Ottosson et al. 2001a), which may simply be explained by that species lack of suitable habitats for fuelling between Lake Chad and the Mediterranean coast.

One big difference, with respect to the foraging situation at Malamfatori, compared to the 1960s, was that we did not observe any „mists" of green midges *Tanytarsus spadiceonotatus*. They seemed to be an important food source for birds during the time of the BOU-expedition, but probably vanished when the lake dried out.

4.2. Potential flight ranges

Many birds take on so much fuel (mostly fat) before the spring departure that it gives them estimated flight ranges of 1700 km or more in still air, enough to reach the Libyan coast. Some birds even carry enough fuel to take them to Italy, more than 2500 km away. This is similar to what has been calculated for spring migrants in Senegal (Ottosson et al. 2001b) and in The Gambia (Hjort et al. 1996). Furthermore, Piersma and van de Sant (1992) showed that spring wind patterns over West Africa at high altitudes (usually above 2500m) could give birds tail winds of about 15 km/h. If we assume an average air speed for these warblers of 30 km/h (e.g. Alerstam 1990, Biebach 1992) this tailwind would give them a ground speed of 45 km/h, which means a range extension of up to 50 %. Although that speed is much slower than the average speed across the Sahara in autumn, (estimated to c. 70 km/h; Biebach et al. 2000), it will allow many birds to cross not only the desert but also the Mediterranean Sea. Some, with especially large fat reserves, may even reach their breeding quarters directly, without re-fuelling (Grattarola et al. 1999).

5. Zusammenfassung

Um mehr über Zugstrategien paläarktischer, trans-Sahara ziehender Vogelarten zu erfahren, haben wir im Frühjahr 1999 und im Frühjahr und Herbst 2000 den Durchzug und die Energetik von Zugvögeln am Tschad-See in NO- Nigeria untersucht. Für sechs Rohrsänger-(*Acrocephalus*) und Grasmücken-(*Sylvia*) Arten lagen genügend Daten für eine Auswertung vor. Diese Daten wurden hinsichtlich inner- und zwischenartlicher Unterschiede im zeitlichen Auftreten, zugzeitlicher Fettdeposition und Flugstrecken analysiert. Beim Abflug im Frühjahr waren die meisten Vögel schwer genug für eine erfolgreiche Wüstenüberquerung und viele so schwer, dass sie damit auch Europa erreichen konnten. Im Herbst dagegen waren die Vögel nach der Wüstenüberquerung mager. Ein Vergleich unserer Ergebnisse mit denen, die in den späten 1960er Jahren in demselben Gebiet gewonnen wurden, macht wahrscheinlich, dass Dorngrasmücken ihre Winterverbreitung südwärts verschoben haben als Folge der inzwischen trockeneren Bedingungen.

6. References

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